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SPECIAL ISSUE: RESEARCH ON THE SOUTH WEST MARGIN OF GONDWANA

First sea turtle remains (Pan-Chelonioidea) from the Eocene of Algarrobo, central Chile

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ABSTRACT: Two isolated bones of sea turtles from Algarrobo, in central Chile, are described. A fragment of a flat element of Ypresian age is identified as part of a right hypoplastron, referable to an indeterminate Pan-Chelonioidea. A second, large fragment from middle-to-upper Eocene levels belonging to the second or fourth left costal of a carapace, preserves distinctive features such as a considerable uniform thickness (5-7 mm), and a prominent ventral rib ridge, plus scute sulci remarkably similar to extant Cheloniidae such as *Chelonia mydas* or *Lepidochelys* spp. Based on these features, it is identified as an indeterminate Pan-Cheloniidae. The studied material represents the first occurrences of sea turtles in the Eocene of central Chile. The different ages of the specimens show the persistence of taxa related to Pan-Chelonioidea throughout the Eocene in the southeastern Pacific, helping to fill the austral geographic gap of the group during the Paleogene.

Keywords: Testudines, South Pacific, Paleogene, Southern Hemisphere, Weddellian Province.

RESUMEN. Primeros restos de tortugas marinas (Pan-Chelonioidea) en el Eoceno de Algarrobo, Chile central. Se describen en esta contribución dos huesos aislados de tortugas marinas procedentes de Algarrobo, en Chile central. Un fragmento de un elemento plano de edad ypresiana se identifica como parte de un hipoplastrón derecho, atribuible a un Pan-Chelonioidea indeterminado. Un segundo fragmento de gran tamaño, procedente de niveles del Eoceno medio a superior, pertenece al segundo o cuarto hueso costal izquierdo de un caparazón, que conserva rasgos distintivos como un considerable grosor uniforme (5-7 mm) y una prominente cresta costal ventral, además de surcos de los escudos notablemente similares a los de Cheloniidae actuales como *Chelonia mydas* o *Lepidochelys* spp. Sobre la base de estas características, se identifica como un Pan-Cheloniidae indeterminado. El material estudiado representa los primeros registros de tortugas marinas en el Eoceno de Chile central. Las diferentes edades de los especímenes demuestran la persistencia de taxones relacionados con Pan-Chelonioidea a lo largo del Eoceno en el Pacífico suroriental, lo que contribuye a llenar el vacío geográfico austral del grupo durante el Paleógeno.

Palabras clave: Testudines, Pacífico sur, Paleógeno, Hemisferio sur, Provincia Weddelliana.

1. Introduction

The fossil record of sea turtles from Chile is sparse and, to date, mostly restricted to few Upper Cretaceous localities in the central part of the country. The oldest such records are known for the lower Maastrichtian of the Valparaíso Region (Suárez *et al.*, 2003; Otero *et al.*, 2012; Otero, 2024a), whereas upper Maastrichtian records are known in at least two localities of the central-south Biobío Region (Biró-Bagóczky, 1982; Gasparini and Biró-Bagóczky, 1986; Karl *et al.*, 1998; Karl and Tichy, 2002; Parham *et al.*, 2014) and in one coeval locality of the central Maule Region (Suárez and Otero, 2008; Otero, 2024a). Despite this known record, unpublished material indicates a geographically broader presence of sea turtles throughout the Late Cretaceous, as suggested by a likely Maastrichtian record from Isla Riesco, Magallanes Region in the south (S. Soto-Acuña, personal communication, 2020), and during the Cenozoic, based on a single Neogene plate from the Bahía Inglesa Formation near Caldera, in the northern Atacama Region (R.A. Otero, personal observation, 2009).

The present contribution describes the first post-Cretaceous sea turtle remains recovered in central Chile (Algarrobo locality). Although fragmentary, the new material helps fill in the geographic and chronostratigraphic gap in the group's presence along the southeastern Pacific.

2. Locality and geologic setting

The coastal town of Algarrobo is in the Valparaíso Region, ~120 km west of Santiago (Fig. 1A). There, two marine units are exposed: the Quebrada Municipalidad beds (Gana *et al.*, 1996), of early Maastrichtian age (Brüggen, 1915; Tavera, 1980; Suárez and Marquardt, 2003), and the Algarrobo beds (Gana *et al.*, 1996). The latter unit was constrained to the middle-to-late Eocene based on biostratigraphy of marine invertebrates,

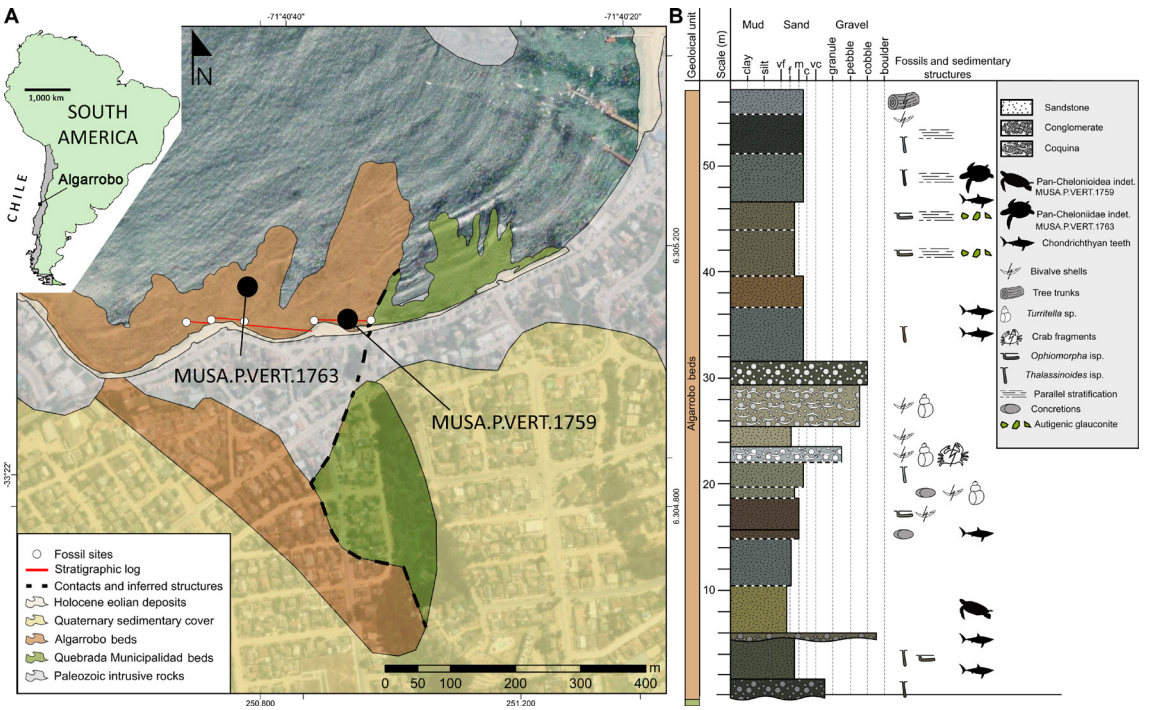

FIG. 1. **A.** Map of Algarrobo, central Chile, indicating the sedimentary units exposed in its coastline and the sample locations. Base satellite image from ArcGIS Pro 3.4 repository. **B.** Stratigraphic log of the Algarrobo beds, reaching ~57 m in thickness, which represents the lower two thirds of the unit. Stratigraphic level colours according to the Munsell Color (2010) soil color charts standard for fresh exposures.

being also correlated with the Millongue Formation (Tavera, 1980). Ongoing studies in the Algarrobo beds show that its basal part extends at least into the Ypresian (Otero, 2024b), so its chronostratigraphic range would cover much of the Eocene series. In addition, it represents a shallow marine to coastal environment proximal to a land drainage outlet.

3. Material and methods

Institutional abbreviations: MMSA.RE, Exhibición, Museo de Historia Natural e Histórico de San Antonio, San Antonio, Chile; **MUSA.P.VERT**, Colección Paleontología de Vertebrados, Museo de Historia Natural e Histórico de San Antonio, San Antonio, Chile; **NTUM-VP**, Vertebrate Paleontology (Laboratory of Evolution and Diversity of Fossil Vertebrates), Museum of Zoology, National Taiwan University, Taipei, Taiwan; **Q**, Museo Geológico Profesor Lajós Biró, Universidad de Concepción, Concepción, Chile; **SGO.PV**, Área de Paleontología, Museo Nacional de Historia Natural, Santiago, Chile; **SMF R**, Forschungsinstitut und Naturmuseum Senkenberg, Frankfurt, Germany.

Material: The two available bones were recovered in different field trips during July 2024 and July 2025, being previously noticed by nearby residents. MUSA.P.VERT.1759 was recovered almost exposed on the surface, requiring minimal mechanical preparation with hand tools. In contrast, MUSA.P.VERT.1763 was extracted partially embedded in the sandstone matrix. The latter was left in a dry environment and protected from direct sunlight in order to dry it naturally. Removal of recent algae on its exposed surface was done with dental tools. The cracked surface was consolidated with B-72, applying especially over the sediment fill between each dorsal crack. After the fossil was naturally dried and cleaned, its preparation was undertaken using the ME-9100 air scribe. A small amount of sediment consolidated with paraloid was left over the ventral surface of the plate to preserve the relative position of the naturally cracked fragments.

Methods: The recovered specimens were compared in terms of their osteology with carapaces of extant sea turtles exhibited in the Museo de Historia Natural e Histórico de San Antonio (MUSA). Taxonomic criteria follow the proposal of Joyce *et al.* (2004). Anatomical nomenclature of the shell follows Zangerl (1969).

4. Results

Systematic paleontology

Diapsida Osborn, 1903
Testudines Batsch, 1788
Cryptodira Cope, 1868
Pan-Chelonioidea Joyce, Parham and Gauthier, 2004

Pan-Chelonioidea indet.
(Fig. 2)

Material: MUSA.P.VERT.1759. Medial fragment of a right hypoplastron.

Locality and horizon: Los Tubos beach, Algarrobo, Valparaíso Region. Algarrobo beds, lower levels. Ypresian (lower Eocene).

Description: The element (Fig. 2A-D) is a flat bone with a consistent thickness of ~5 mm. The larger preserved suture (identified here as the anterior margin) is highly indented but retains a generally straight outline. The adjacent lateral margin (identified here as the medial margin) shows two prominent projections. The other two remaining margins (lateral and posterior) are eroded. The ventral (external) surface of the bone shows a notch over its medial half. The opposite surface (dorsal/internal) is flat, without noticeable structures. Several cracks are present on this side.

Laterality and anatomical identification: A ventral notch over the ventral surface of the hypoplastron (Fig. 2D, E) is a feature illustrated by Liaw *et al.* (2025, fig. 2E) for *Lepidochelys olivacea* (NTUM-VP 2205281), although the anatomical description of this feature is commonly ignored. Four stellate projections appear as short elements, because these are incompletely preserved (distal tip missing). The small size of the bone also correlates with a young individual where stellate projections could be briefly developed on early ontogenetic stages. Nonetheless, the two preserved projections (plus two others only represented by their broken attachments) in MUSA.P.VERT.1759 are consistent with the stellate pattern (lateral cornua) of plastral elements (*i.e.*, hyoplastron and hypoplastron) among Pan-Chelonioidea (Lehman and Tomlinson, 2004). The preserved sutured straight margin, the articular facet and the stellate projections are all consistent with landmarks present over the right hypoplastron of fossil and extant sea turtles (Hirayama, 1997, figs. 1-5; Wyneken, 2001, fig. 97).

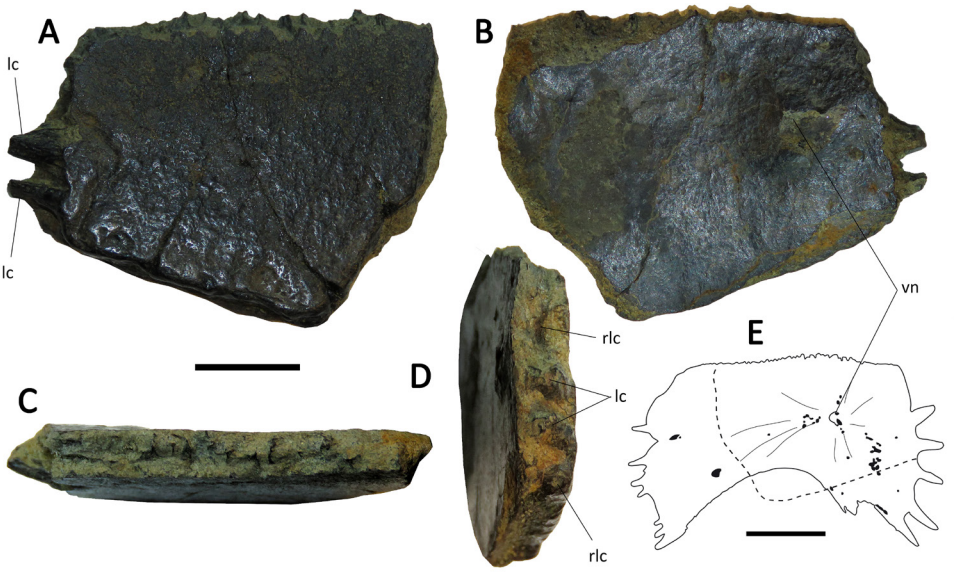

FIG. 2. **A-D.** MUSA.P.VERT.1759: Pan-Chelonioidea indet. Fragment of a right hypoplastron in dorsal (internal) view (A). Same element in ventral (external) view (B). Anterior profile of the sutural contact with the hypoplastron (C). View of the medial profile, indicating the preserved stellate projections (lateral cornua), as well as those broken and missing (D). **E.** Outline of the right hypoplastron of *Lepidochelys olivacea*, representing the relative overlapping of the portion preserved in MUSA.P.VERT.1759 (the general hypoplastron morphology slightly differs between the two); sketch modified from Liaw *et al.* (2025, fig. 2E). Anatomical abbreviations: **lc**, lateral cornua (stellate projections); **rlc**, remains of lateral cornua; **vn**, ventral notch. A-D, scale bar equals 10 mm; E, scale bar equals 5 cm.

Referral to Pan-Chelonioidea: The almost straight anterior margin of the hypoplastron (hyoplastron/hypoplastron suture) and the presence of medial projections are features present among extant Pan-Cheloniidae (Wyneken, 2001, fig. 97; Cáceres *et al.*, 2018, fig. 6). Similar topologies are also present among fossil forms including Protostegidae, Toxochelyidae and stem Dermochelyidae (Hirayama, 1997), with some taxa having a hyoplastron/hypoplastron suture interrupted by a medial fossa (*e.g.*, *Toxochelys latiremis*, *Allopleuron hofmanni*, *Santanachelys gaffneyi*, *Protostega gigas*; see Hirayama, 1997, figs. 1-3 and 5). Although incomplete, MUSA.P.VERT.1759 preserves its anteromedial margin that proves the lack of a medial fossa, being more similar to extant pancheloniids of the genera *Lepidochelys* and *Natator* (Lehman and Tomlinson, 2004, fig. 6). Due to its incompleteness, the studied material is kept as an indeterminate Pan-Chelonioidea, although it shows affinities to Pan-Cheloniidae.

A freshwater erratic origin of MUSA.P.VERT.1759 cannot be ruled out, but the accumulated evidence regarding the environment of the unit (see Discussion, below) makes a continental provenance unlikely.

Pan-Cheloniidae Joyce, Parham and Gauthier, 2004

Pan-Cheloniidae indet.
(Fig. 3)

Material: MUSA.P.VERT.1763. Second or fourth left costal (rib).

Locality and horizon: Los Tubos beach, Algarrobo, Valparaíso Region. Algarrobo beds, upper levels. Middle-to-upper Eocene.

Description: The general contour of the costal is rectangular (Fig. 3A, B). Its ventral surface preserves the rib head (Fig. 3C, D), while the midline rib ridge is partially crushed. The dorsal surface of the costal is cracked in several parts and along its mid portion, showing remains of an axial sulcus (sulcus between two successive lateral scutes). In its medial portion, the lateral sulcus of a large vertebral scute is partially preserved. The medial and anterior margins of the costal are almost complete. The first shows the sutural contact with at least two neural plates (Fig. 3B, D), one of them covering about two thirds of the plate cranio-caudal length. The remaining medial outline for the following neural plate shows a different angle with regard to the

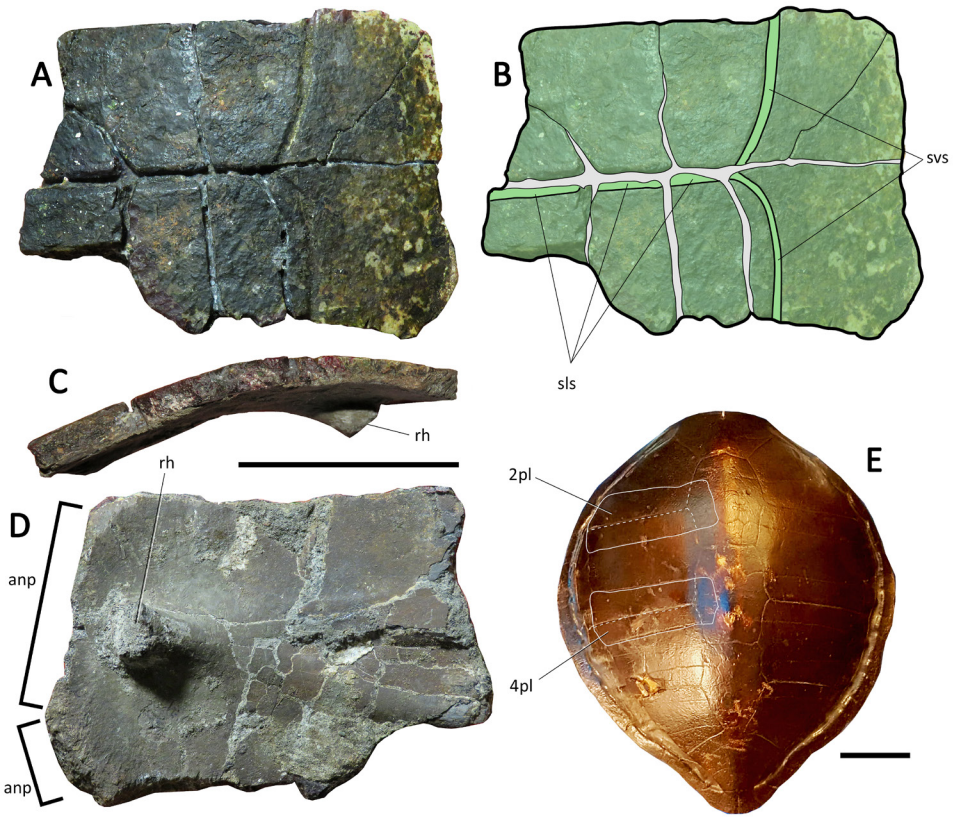

FIG. 3. **A-D.** MUSA.P.VERT.1763: Pan-Cheloniidae indet. Second or fourth left costal in dorsal view (A). Anatomical schematic, highlighting the preserved sulci (light green) (B). Same element in craniocaudal profile (C). Ventral (internal) view (D). **E.** Carapace of *Chelonia mydas* (MMSA.RE.022, in exhibition at MUSA, 2025) indicating the position of the second and fourth costals in white contour. Dashed white lines indicate the sulci associated with the limits of the dermal scutes. Anatomical abbreviations: **2pl**, second costal; **4pl**, fourth costal; **anp**, articulation with neural plate; **rh**, rib head; **sls**, sulcus between lateral scutes; **svs**, lateral sulcus of the respective vertebral scute. A-D, scale bar equals 5 cm; E, scale bar equals 10 cm.

almost straight, anterior, larger neural element. The pleural thickness is uniform and reaches 5 to 7 mm.

Laterality and anatomical identification: The straight rib head and its respective ventral shaft preclude a posterior position of the plate, considering that rib heads and shafts become posteriorly curved in the posterior half of the carapace (Márquez, 1990, fig. 11; Wyneken, 2001, fig. 93a, b). The plate also has a medial sulcus consistently orientated with the rib shaft (Fig. 3A, B). The partial vertebral scute scar can be separated into two halves, each one with a different contour. Both halves have a similar cranio-caudal orientation, again precluding a posterior position in the carapace, considering that the vertebral scute margins acquire comparatively more acute angles in posterior positions (Wyneken, 2001, p. 4). The curvature observed in lateral profile, plus the ~100° angle between the neural suture and the unique complete axial margin, suggests that this costal is part of the anterior, left side of the carapace. Compared to the extant carapace of *Chelonia mydas*, the sulci for the vertebral plate are similar to those present in the dorsal surface of the second and fourth costal (Fig. 3E), reason why MUSA.P.VERT.1763 is identified as one of these element.

Referral to Pan-Cheloniidae: MUSA.P.VERT.1763 possesses a uniform, considerable thickness reaching 5 to 7 mm along the entire available plate. The presence of a ventral rib ridge (crushed but visible) extended along the entire preserved costal fragment strongly suggests that the rib shaft extended beyond the lateral margin, thus forming a fenestration between

the costal and the peripherical plates. These traits have been considered typical of Pan-Cheloniidae (Joyce *et al.*, 2004; Cadena *et al.*, 2018). Based on these features, MUSA.P.VERT.1763 is here referred to as Pan-Cheloniidae. The incompleteness of the material precludes a genus referral.

Comparisons: Among extant sea turtles (except *Dermochelys coriacea*), the lateral outline of the vertebral scutes is variable. Several factors including ontogenetic stage, sexual dimorphism, and even epigenetic factors may lead to allometries on the scute outlines (Casale *et al.*, 2017). However, this variability is not linked to topology changes between the dermal scutes and the underlying bony elements. Thus, it is possible to assess the relative position of the scutes on the basis of the sulci preserved on the dorsal surface of MUSA.P.VERT.1763.

In this sense, second/fourth vertebral scutes with sharp lateral projections (as those interpreted from MUSA.P.VERT.1763 preserved dorsal sulci) are commonly present among adult individuals of the hawksbill turtle (*Eretmochelys imbricata*; Márquez, 1990, fig. 30) and in the loggerhead turtle (*Caretta caretta*; Márquez, 1990, fig. 23). On the contrary, vertebral scutes with comparatively straighter lateral outlines and similar to those of MUSA.P.VERT.1763 are present in the green turtle (*Chelonia mydas*; *e.g.*, MMSA.RE.022) (Fig. 3E), Kemp's ridley turtle (*Lepidochelys kempii*; Márquez, 1990, fig. 33), and the olive ridley turtle (*Lepidochelys olivacea*; Márquez, 1990, figs. 15-21).

5. Discussion

Environment of the studied material: The Algarrobo beds unit was undoubtfully deposited in a marine environment, as evidenced by the abundant *in situ* invertebrate fauna (Philippi, 1887; Brüggen, 1915; Tavera, 1980). Previous records of marine vertebrates in the unit have been represented exclusively by marine forms (*i.e.*, chondrichthyans; Suárez and Marquardt, 2003), including recently recognized pelagic shark taxa (*Striatolamia macrota*, *Cretolamna* sp., *Xiphodolamia* sp.; Otero *et al.*, in press). While fragmentary driftwood is present, the material is mostly represented by small chips and rarely by centimetric trunk fragments invaded by *Teredolites* isp. (Tavera, 1980), the latter indicative of a long-term buoyancy. On the other hand, the unit includes some levels with *in situ* banks of the gastropod '*Turritella*' *landbecki* (Tavera, 1980). Regarding taphonomy, well-preserved chelipeds and appendicular elements of decapods (Schweitzer *et al.*, 2006), plus chondrichthyan teeth with well-preserved delicate cusplets (Otero *et al.*, in press), supports a general *in situ* occurrence of both benthic and nektonic organisms (thus, including the material here studied).

Previous sea turtle fossil record from Chile: Gasparini and Biró-Bagóczky (1986) described a mandible (Q.377), firstly referred to as *Osteopygis* sp. (currently, genus *Euclastes*), from probable upper Maastrichtian beds of the Quiriquina Formation, in the Biobío Region. A skull without mandible (SMF R 415) from the same unit was referred to as *Osteopygoides* aff. *sculptus* by Karl *et al.* (1998). The same specimen was later considered a Baenidae and reassessed as *Australobaena chilensis* by Karl and Tichy (2002). Suárez *et al.* (2003) mentioned plates and figured a fragmentary humerus from lower Maastrichtian beds in Algarrobo. Later, Suárez and Otero (2008) described fragmentary plates referred to as Chelonioidea indet. (SGO.PV.6503 and 6504) from upper Maastrichtian beds of the Quiriquina Formation in Loanco, Maule Region. Then, complementary material (SGO.PV.6573 and 6768) from the lower Maastrichtian of Algarrobo was initially referred to as cf. Dermochelyidae indet. (Otero *et al.*, 2012) and more recently to *Mesodermochelys* sp. (Otero, 2024a). Parham *et al.* (2014) described a new skull (SGO.PV.6504) of the genus *Euclastes*, from upper Maastrichtian levels of the Quiriquina Formation exposed in Cocholgüe, Biobío Region. Parham *et al.* (2014) discussed the taxonomic status of *Australobaena chilensis*, expressing doubts about the genus and species referral. They also commented that its skull as well as the jaw described by Gasparini and Biró-Bagóczky (1986) indeed matched the relative bone proportions of the genus *Euclastes.* Karl *et al.* (2024) re-described the skull of *Australobaena chilensis* using photographs, adopting the family-level referral to Pan-Cheloniidae as previously proposed by Parham *et al.* (2014).

In summary, the Upper Cretaceous sea turtle record from central Chile is to date characterized exclusively by Pan-Chelonioidea of the clades Euclastidae (*sensu* Lapparent de Broin *et al.*, 2025) and Dermochelyidae (=Pandermochelys, *sensu* Joyce *et al.*, 2004). The new discoveries signify the local

presence of Pan-Cheloniidae (at least) beginning in the Ypresian. While MUSA.P.VERT.1763 cannot be assigned to any genus due to its incompleteness, its broad shape contacting both anterior and posterior successive costals, plus the sulci for the vertebral scutes, obviates its referral as Dermochelyidae. The latter clade has a soft carapace lacking large dermal scutes, while the bony carapace is conformed by a mosaic of small ossicles instead of cranio-caudally extended costal bones (Márquez, 1990; Wyneken, 2001).

Paleobiogeography: In South America, Cenozoic Pan-Cheloniidae are documented in the Paleocene of Argentine Patagonia with the species *Erquelinnesia meridionalis* (de la Fuente and Casadío, 2000; after Parham and Pyenson, 2010), with a major local gap during the Eocene. Geographically closer to the study area, Eocene records are represented by remains of indeterminate Dermochelyidae from southernmost South America (Bona *et al.*, 2024), and the Antarctic Peninsula (de la Fuente *et al.*, 1995; Albright *et al.*, 2003). Few Oligocene records are known along the southeastern Pacific: in Peru, undescribed sea turtle remains from the Oligocene-Miocene (Brand *et al.*, 2011; Cadena *et al.*, 2018) have been recognized, as well as remains of an indeterminate Pan-Cheloniidae of late Oligocene age (Cadena *et al.*, 2018). Miocene Pan-Chelonioidea are documented in Peru, with the species *Pacifichelys urbinai* Parham and Pyenson, 2010, and the dermochelyid *Natemys peruvianus* Wood *et al.*, 1996. In Chile, there is unpublished material from the Miocene of the Navidad Formation (housed at Museo Nacional de Historia Natural, Santiago, Chile) and the Miocene-Pliocene Bahía Inglesa Formation (housed in the Museo Paleontológico de Caldera), which likely represent additional records of Pan-Cheloniidae (R.A. Otero, personal observation, 2009).

The specimens studied here represent the very first Eocene records of sea turtles in the southeastern Pacific, adding to other coeval records from the Austral basin of southern South America, the Antarctic Peninsula, and New Zealand. These records, to date, are mostly represented by indeterminate Dermochelyidae (de la Fuente *et al.*, 1995; Köhler, 1995; Albright *et al.*, 2003; Bona *et al.*, 2024), and eventually by forms resembling Pan-Cheloniidae, based on the presence of well-ossified peripheral plates (see Bona *et al.*, 2010).

6. Conclusions

This contribution presents two fragmentary bones of sea turtles recovered from the Paleogene Algarrobo beds, at Algarrobo, central Chile. A partial right hypoplastron from Ypresian levels is here referred to as an indeterminate Pan-Chelonioidea, showing affinities to extant Pan-Cheloniidae. A second, larger plate from middle-to-upper Eocene levels, is here identified as the second or fourth left pleural, based on its distinctive sulci for the vertebral scutes, similar to those present in extant representatives of the genus *Lepidochelys* and in *Chelonia mydas*.

The described material represents the first record of Pan-Chelonioidea/Pan-Cheloniidae sea turtles in the Eocene of the southeastern Pacific, helping to fill a major geographic and chronostratigraphic gap in the austral fossil record of the group. The current specimens also increase the austral diversity by adding the first confirmed Eocene non-Dermochelyidae sea turtles of the southern hemisphere. It also extends the continuous presence of Pan-Cheloniidae along the southeastern Pacific at least from the Ypresian to the Neogene, based on previous, northern records.

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